70—4

Proceedings of the American Academy of Arts and Sciences.

Vol. 70. No. 4.—May, 1935

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With Two Plates.

(Continued from page 3 of cover.)

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Received February 4, 1935 Presented February 13, 1935

Among the Orthopteroid insects which Sellards described from the Elmo limestone in 1909 there were several closely related species which he placed in two families, Lemmatophoridae and Ortadae, and assigned to the Order Protorthoptera. In 1928, after working over the fossils in the Yale collection from this formation, Tillyard redescribed and revised the arrangement of these species, establishing for them the new order Protoperlaria, characterized by the presence of wing-like prothoracic expansions and considered by him to be allied and ancestral to the Recent stone-flies (Perlaria).

These species make up a very large part of the insect-fauna of the Elmo limestone, including at least twenty per cent of all the specimens which have been collected. In the Yale collection Tillyard found about 210 specimens; in the Sellards collection I find 42 specimens (in addition to the types), and in the Harvard collection more than 600 specimens. The occurrence of so many individuals is almost certainly due in large measure to the fact that these species were aquatic in the nymphal stages and bred in the same body of water which deposited the limestone in which they are preserved. That such was the case is demonstrated by the presence of many nymphs which undoubtedly belong to these insects.

This large series of fossils, representing only seven species, has enabled us to ascertain a great deal more about their body structure than is usually the case with fossil insects; in fact, we can safely say that at least two of these species are more completely known than any other extinct insects which have been found, with the possible exception of some of those preserved in the Tertiary ambers. Such a knowledge of the body structure is particularly helpful in the study of these specific fossils, since their position in the Orthopteroid series of insects would not otherwise be clear. It is mainly because of our lack of knowledge of the body structure of the Palaeozoic Orthopteroids in general that the classification and relationships of those insects are so obscure and the Order Protorthoptera merely a heterogeneous

[1] This series of studies has been aided by grants from the Carnegie Foundation, the National Academy of Sciences, and the Milton Fund of Harvard University.

mixture of species of uncertain affinities. Sellards was perfectly justified, therefore, in placing the fossils now known as Protoperlaria within the Protorthoptera, since he knew nothing of their body structure; and since in the Elmo limestone there are many Orthopteroid insects, apparently Protorthoptera in the true meaning of the word, possessing wings almost identical with those of the Protoperlaria.

Martynov, in the course of his study of the Permian insects of Russia, was so impressed by the similarity between the wings of the Lemmatophoridae (including the Ortadae) and those of several other families of Orthopteroid insects in the Kansan and Russian Permian, that he grouped all of these families into a new order, Miomoptera (1927). Tillyard, however, contends (1928) that the Order Miomoptera is only another assemblage of unrelated forms, established upon specific and even individual characteristics. In 1930, after a description of additional fossils from the Permian of Russia, Martynov redefined the order Miomoptera and maintained that the various families included in that order (Atactophlebiidae, Lemmatophoridae, Liomopteridae, Probnisidae, and Palaeomantidae) are really closely related to each other and "differ chiefly in the degree of specialization and reduction of the wing-venation."

The principal weakness in Martynov's view lies in the nature of the evidence which he uses to demonstrate the close relationship between the several families of the order Miomoptera. As he himself states, this relationship is expressed chiefly in the degree of specialization and reduction of the wing venation, without regard for the rest of the anatomy of the insects concerned. Of the five families included in the order, one, Probnisidae, is known to Martynov only by Sellards' superficial description of the wings; and the same is true of the Liomopteridae, although Martynov also placed here one hind wing (Haplopterum) from the Russian Permian. The family Lemmatophoridae, which has been discussed by Tillyard (1928), was known to Martynov at the time when he originally established the order Miomoptera (1927) only by Sellards' brief description of the wings. The family Atactophlebiidae is known by the wings of one species from the Russian Permian; and the family Palaeomantidae, although present in both the Russian and the Kansan Permian, is chiefly represented by wings, only a few body structures having been found.[2] Fortunately, in the collection of Kansan Permian insects at the

[2] In Part 6 of this series of papers (1933) I reviewed the evidence which indicated that the family Palaeomantidae (Delopteridae) was actually a member of the order Copeognatha, as originally believed by Tillyard.

Museum of Comparative Zoology there are many specimens of Liomopteridae and Probnisidae and related families which show the body structure in complete detail. A study of these specimens has convinced me that Martynov's attempt to place the three families Lemmatophoridae, Probnisidae, and Liomopteridae in a single order is not justifiable. The evidence for this conclusion will not be presented here, but will be reserved for a subsequent paper in this series dealing with the two latter families.

In any discussion of Palaeozoic Orthopteroids, however, it should be borne in mind that there is room for considerable difference of opinion regarding the limits of the various orders and other taxonomic divisions; for these particular ancient insects are very close to the progenitors of many of our existing orders, which although perhaps more or less widely divergent at present, converge rapidly as we go back through the Mesozoic, and nearly, if not actually, meet in the Lower Permian. In this case, it is not merely lack of complete knowledge of the extinct insect's anatomy which gives rise to different opinions of its affinities, but the difficulty of drawing lines between one group and another.

Some diversity of opinion has arisen over the ordinal name of the Lemmatophoridae. Tillyard claims (1928, p. 348) that his name Protoperlaria takes priority over Martynov's name Miomoptera (1927) for an order based wholly or partly on the Lemmatophoridae, since he published a photograph of a specimen of Lemmatophora in 1926, stating in the caption under the photograph that it was a representative of a new order, Protoperlaria. Martynov, however, contends (1930) that since Tillyard's paper did not contain any diagnosis of the order, the name Miomoptera proposed by him in 1927 has priority over Protoperlaria, which was not formally proposed until 1928. Unfortunately, the question of the priority of ordinal names is not considered in the Code of Zoological Nomenclature, but I believe that Tillyard's stand is the more logical one. In this connection, it is a matter of much significance that Tillyard and Martynov had in mind two very different orders of insects. Tillyard conceived the Protoperlaria as typically represented by the family Lemmatophoridae, and as ancestral only to the Recent Perlaria. Martynov, on the other hand, had in mind an order typically represented by the peculiar family Delopteridae (Palaeomantidae), and ancestral to the Embidaria, as well as the Perlaria, and various extinct families.[3]

[3] For a discussion of the relationships and synonymy of the family Delopteridae, see part 6 of this series, p. 450–461 (Proc. Amer. Acad. Arts and Sciences, **68** (11), 1933).

Since, as I shall show below, the members of the family Lemmatophoridae are so far removed structurally from the other Permian Orthopteroids that they require a separate order for their reception, it seems logical to use the name Protoperlaria for that order rather than Miomoptera.

Although Tillyard has already given a diagnosis of the order Protoperlaria, it is necessary for us to revise many of his statements and to redefine the ordinal characteristics. He considered the wing-like expansions on the prothorax of these insects to be an ordinal feature, asserting (1928, p. 186) that such organs are never found in the true Protorthoptera and are previously known only in the Palaeodictyoptera and Protohemiptera. But having worked over all of the Permian insects in the Harvard collection, I find that the majority of the Orthopteroid insects in the Elmo limestone possessed prothoracic lobes fully as large as those of the Lemmatophoridae. The presence of these lobes in the various Permian Orthopteroid insects and the similarity of their wing venation to that of the Lemmatophoridae greatly increases the difficulty of separating the latter insects from the former, and is a strong point in favor of grouping them all in one order, as was done by Martynov. The obvious step, perhaps, would be to place all these species possessing prothoracic expansions into the order Protoperlaria, conforming with Tillyard's original view of the occurrence of the lobes in these insects. But a study of the undescribed Permian Orthopteroids in the Harvard collection, including those with the prothoracic expansions and a wing venation similar to that of the Lemmatophoridae, reveals the fact that most of the families, if not all, *consist of species with a fully developed external ovipositor in the female*. The presence of an ovipositor in these insects is of great significance, since it demonstrates that their mode of development was entirely different from that of the Lemmatophoridae, which (like the Perlaria) not only lacked an external ovipositor, but were aquatic in the nymphal stages. It seems to me, therefore, advisable to restrict the order Protoperlaria to include only the species that lacked an ovipositor and were aquatic in the nymphal stages, since these clearly were in the direct evolutionary line or very nearly in the direct line of the Perlaria; whereas the other Orthopteroid insects, which possessed an ovipositor, were part of a very different branch of the Orthopteroidea, leading to the true Orthoptera.

Restricted in this way, the Order Protoperlaria includes a series of small and medium sized insects, having a wing expanse of ten to forty

millimeters. The antennae were long and multisegmented; eyes large but not so prominent as in existing Perlaria; ocelli were probably present. The prothorax possessed a pair of wing-like lobes, covered with hairs. The meso- and metathoracic segments were large and flattened. The venation of the fore wing was simple: Sc terminated on the costal margin beyond the middle of the wing and was connected to the margin by a series of oblique cross-veins; Rl was unbranched, Rs either simple or forked or occasionally three-branched; both MA and MP were present, MA being unbranched (rarely forked), MP being either simple or forked or even three-branched; the proximal half of MP was obsolescent in all species; CuA was a very strong vein, having three and occasionally four branches (rarely only two); CuP was obsolescent, being reduced to a straight *vena dividens*. 1A and 2A were present. The hind wing was slightly shorter than the fore but had an enlarged anal area. Sc terminated on the costal margin and costal veinlets were probably present in some species; Rl was unbranched, Rs either simple or forked; MA was unbranched, MP either simple or forked; CuA was a strong vein, but reduced to two branches; CuP was very weak and obsolescent; the anal fan contained four main mains, consisting of 1A and derivatives of 2A; the first branch of 2A was forked. The venation of both wings, but of the fore pair especially, was very variable within the species, particularly in the amount of fusion between MA and Rs. *The tarsi of all legs were 5-segmented* (not 3-segmented, as stated by Tillyard); the hind legs were considerably longer than the others. The abdomen was rather small in comparison with the rest of the body and contained ten segments visible from above, the first nine segments bearing (in some species at least) a pair of small lateral processes resembling vestigial gills. Cerci were present and well developed. The nymphs were aquatic and resembled in general structure the nymphs of Recent Perlaria; they possessed well developed lateral abdominal gills.

The order Protoperlaria, as defined above, includes only the family Lemmatophoridae, from the Lower Permian of Kansas. Martynov (1930, p. 1116) has placed in this family the genus Kazanella, with two species (*rotundipennis* Mart. and *compressa* Mart.), both known only from fragments of wings. These wings, however, are almost identical with those belonging to certain of the undescribed Orthopteroids from the Lower Permian in the Harvard collection which possess the ovipositor previously mentioned. I therefore exclude Kazanella from the family Lemmatophoridae and the Protoperlaria as a whole, and refer it to the Protorthoptera. G. Zalessky (1933, p. 129) has also included in

this order the family Caenoptilonidae, containing the single species *Caenoptilon minutum* Zall., from the Permian of Russia. The unique specimen on which this species was based is so poorly preserved and so badly distorted, as indicated by the waved and jumbled veins in Zalesky's figure, that its assignment to any order is uncertain. At any rate, it is not a member of the Protoperlaria, as this group is defined above.

At present there seem to be but five genera in the family Lemmatophoridae: Lemmatophora, Lisca, Artinska, Paraprisca, and Lecorium, all erected by Sellards in 1909. Several other genera as well as families were also established by Sellards for species now included in the Lemmatophoridae, but these were based entirely upon individual variations, resulting from the marked instability of the venation. In 1927, with the aid of a grant from the National Academy of Sciences, I was enabled to study Sellards' type specimens at Austin, Texas, and subsequently sent photographs of the types to Dr. Tillyard, who with their aid straightened out the taxonomy of Sellards' species (Tillyard, 1928). I agree with his conclusions on the synonomy of these genera except for that regarding Lisca, which he synonymized with Lemmatophora. He also erected a new genus, Sellardsia, but this is undoubtedly identical with Lecorium, as I shall show later. The five genera mentioned above fall readily into the two following groups, which for convenience I designate as subfamilies:

I. Subfamily **Lemmatophorinae.** Fore wings broad, their length being about two and one-half times their width, never three times; hind wing with a deep incision on the margin at the termination of CuP; prothoracic lobes large, extending over the anterior half of the mesothorax.

1. Radial sector forked ..... *Artinska*
   Radial sector unbranched 2

2. Subcosta remote from costal margin at the base of the wing; radial sector arising at about the middle of the wing; Rl of fore wing with a slight upward bend at the origin of the radial sector; Rl straight in pterostigmal region; cerci long; hind tarsal segments unequal in length ..... *Lemmatophora*

   Subcosta close to costal margin at base of fore wing; radial sector of fore wing arising well proximad of the middle of wing; Rl not bent at the origin of Rs; Rl curved in pterostigmal region; cerci short; hind tarsal segments equal ..... *Lisca*

II. Subfamily **Parapriscinae.** Fore wings narrow, their length being more than three times the width and sometimes nearly four times; hind wing with only a slight incision on the hind margin at the termination of CuP, the margin of the anal area being almost continuous with the rest of the wing margin; prothoracic lobes small, hardly reaching to one-fourth the length of the mesothorax.

Rl straight, not bent at the origin of the radial sector, not curved in the pterostigmal region; CuA entirely free from M; all legs slender, the hind pair tenuate; cerci short, about one half the length of the abdomen..... *Paraprisca*

Rl bent slightly at origin of the radial sector and curved in pterostigmal region; CuA always coalesced with M; all legs stout; cerci fully as long as abdomen..... *Lecorium*

Subfamily LEMMATOPHORINAE.

Genus *Lemmatophora* Sellards.

Lemmatophora Sellards, 1909, Amer. Journ. Sci., (4) **27:** 162.
Lemmatophora Tillyard, 1928, Amer. Journ. Sct., (5) **16:** 187.

Fore wing: broad, costal margin curved, apex rounded; Sc remote from margin at the base, terminating at the proximal end of the pterostigma; R straight as far as the origin of Rs, at which point Rl diverges upwards slightly and then makes an abrupt downward bend at the proximal end of the pterostigma; Rs unbranched; MA unbranched, rarely forked, arising near the middle of the wing; MP forked (rarely 3-branched). *Hind wing:* very broad, costal margin nearly striaght, apex bluntly rounded, hind margin with a deep incision at end of CuP; Rl curved below the pterostigmal region; Rs unbranched, originating near the middle of the wing and coalescing with MA for a short distance; MA unbranched; first branch of 2A forked.

Body structure: antennae short, only a little longer than the head and thorax combined, all segments except the first two subequal; front and middle legs short, hind legs much longer; first segment of hind tarsus much longer than the other segments; cerci long.

The genotype of Lemmatophora is *L. typa* Sellards. In my opinion this is the only species in the genus, although Tillyard has placed here *Lisca minuta* Sellards. In view of the very different body structure of the two insects, however, I believe that the species are generically distinct.

Lemmatophora typa Sellards.

Figure 1; plate 1, fig. 1; plate 2, fig. 3, 4.

Lemmatophora typa Sellards, 1909, Amer. Journ. Sci., (4) **27:** 162.
Lemmatophora typica Tillyard,[4] 1928, Amer. Journ. Sci., (5) **16:** 191.
Lemmatophora typica Tillyard, 1928, *ibid.*, p. 318 (full synonymy given here and in the preceding reference).

Fore wing: length 5.5–9 mm.; width, 2.0–3.3 mm.; Sc close to R at the base of the wing; 9–16 veinlets in the wide costal space; pterostigmal region usually traversed by several veinlets, greatly variable in shape and number; two strong cross-veins between Sc and R; 4–6 cross-veins between Rs and R1; one of these sometimes very oblique and long, having much the appearance of a branch of Rs; MA originating proximad of the origin of Rs, nearly always unbranched and generally free but occasionally coalesced with Rs for a variable distance; MP usually deeply forked; CuA formed in the manner characteristic of the genus, there being considerable variation in the length of the branches; occasionally CuA bears four branches or is reduced to two; at the first fork of CuA there are two or three prominent cross-veins leading to M; the two anal veins are divergent and are connected by two stout cross-veins, the outer one sigmoidally curved. *Hind wing:* length, 5.7–8.4 mm. Sc remote from the margin at the base, and even further away near its middle point; about 6 weak costal veinlets; pterostigma well developed; Rs arising a little proximad of the middle of the wing and soon fusing with MP for a short distance; MA arising almost directly below the origin of Rs; MP continuing in a straight line the basal part of M; CuA arising at the very base of the wing and soon fusing with M for a short distance, forking directly below the origin of Rs; CuP a straight and weak vein, not very concave and distally crowded between CuA2 and 1A.

The fore wings of most of the specimens have indications of color markings and probably those wings which do not show such coloration have lost it during the course of preservation. The arrangement of the markings is clearly shown in the photograph in figure 1, plate 1. The most prominent spot is the one at the first fork in CuA; the others are more variable in position and extent, and those margining the cross-veins may be entirely absent. Well preserved specimens

[4] Tillyard (1928) changed the name of this insect to *typica* on the grounds that there is no such word as *typa*. Since there is nothing in the Zoological Code of Nomenclature which permits change to be made on this basis, I have used Sellards' original name.

also show that the wing surface was heavily covered with microtrichia, as in all the other Protoperlaria.

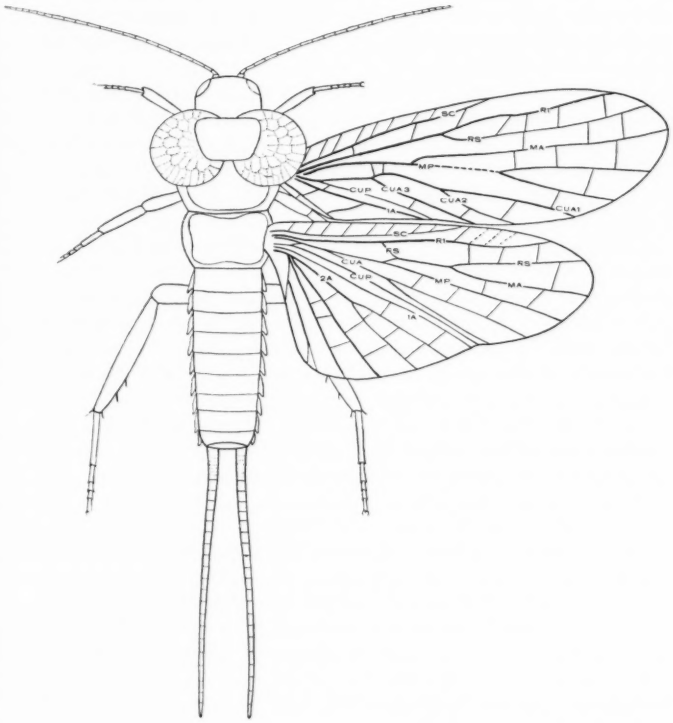

FIGURE 1. Reconstruction of *Lemmatophora typa* Sellards, based mainly on specimen No. 3536*ab*, Museum of Comparative Zoology. Sc, subcosta (−); Rl, radius (+); Rs, radial sector (−); MA, anterior media (+); MP, posterior media (−); CuA, anterior cubitus (+); CuP, posterior cubitus (−); 1A, first anal (+); 2A, second anal (+).

Body structure: length of body, including cerci, 11–13 mm.; length of antennae 5 mm., and of cerci, 5 mm. Antennae with 23–25 segments; first tarsal segment of the fore and middle legs equal in length

to the combined third and fourth, which are subequal; last segment twice as long as the fourth; hind tibia at least twice as long as the middle and fore tibia and somewhat swollen; first tarsal segment of hind leg as long as the rest of the tarsus, second segment as long as the third and fourth combined, which are equal; last segment about the same length as the second.

The holotype of this insect was a fore wing, No. 1162 in the Sellards collection. Since this specimen (as well as the types of the synonymous species) has been lost, I designate as the neotype specimen No. 3536ab in the Museum of Comparative Zoology; this consists of a complete insect (plate 1, figure 1), collected by the writer in the lower layer of the limestone in 1927.

Lemmatophora typa is unquestionably the commonest insect in the Elmo limestone. In the Yale collection there are 86 specimens, in the Sellards collection (in addition to the original types) 25, and in the collection of the Museum of Comparative Zoology more than two hundred specimens, making a total of well over three hundred individuals of this species. Adult specimens are only about half as numerous in the upper layer as in the lower layer of limestone, although nymphal forms which probably belong to this species are much commoner in the upper. The following are the more important specimens in the Harvard collection; all are from the lower layer of limestone except No. 3541ab. Nos. 3527, 3528, 3529ab, 3530ab, 3531ab, 3535ab, and 3541ab, all perfectly preserved fore wings; No. 3532ab, consisting of fore and hind wings, and portions of the body, the prothoracic lobes being very clear; No. 3533ab, one fore wing and part of the body; 3536ab, the neotype, a very nearly complete insect, showing fore and hind wings, general body structure, one complete antenna, one fore leg and one hind leg (see figure 1, plate 1); No. 3537ab, nearly a complete insect, showing two fore wings and most of hind wings, general body structure, both antennae, one middle and both hind legs; No. 3538ab, portions of wings and the body, the antennae being especially fine; No. 3539, nearly complete, showing particularly well the thorax and the prothoracic wing pads; No. 3540ab, portions of the wings and body; 3542, the wings and several parts of the body; 3543ab, one fore wing, head, one antenna, and thorax, all body parts being perfectly preserved; 3544ab, one fore wing and portions of the abdomen, the cerci being complete; 3545ab, fore and hind wings, and portions of the body, the head, cerci and prothoracic lobes being very clear; No. 3547, fore wing, portions of thorax and head; 3548ab, fore wing, thorax and head (excellent);

No. 3549ab, fore and hind wings and almost the whole body, showing especially well the prothoracic lobes and head. In the Sellards collection there are three specimens of fore wings which are complete and very well preserved: Nos. 697, 331, and 329.

There are several features of the body structure of this insect which are of much interest. Some of these have been already mentioned by Tillyard, but the collection in the Museum of Comparative Zoology is so rich in specimens showing the body that I have considered it advisable to add a short discussion of this subject:

1. Head. In none of the specimens which I have seen, including those in the Yale collection at the Peabody Museum, has it been possible for me to make out a satisfactory frontal view of the head, although this has been figured by Tillyard in his account of the Yale fossils. All the Harvard specimens which are preserved in a dorsal-ventral position have the head in an attitude corresponding to that usually found in Recent Perlids, the frontal region being hidden from above. The maxillary palpi are preserved in several specimens in lateral position and they appear to be 4- or 5-segmented. The eyes, although large, do not protrude nearly as much as in the Perlaria and they are situated further forward.

2. Thorax. The pronotum is large and subcordate; the remainder of the prothorax is covered by the large prothoracic lobes. The latter are not attached merely to the sides of the pronotum, but extend nearly to the mid-line in the front and rear. These lobes almost certainly arise from beneath the pronotum itself, as can easily be seen in specimens preserved in a lateral position. Their reticulated network has all the appearances of being formed of true veins, but it is more likely composed of pigment bands, as suggested by Tillyard; at any rate, the size and arrangement of the cellules forming the network is very variable. The whole surface of the lobes is covered with minute hairs. The mesonotum is flat and subcircular; it conceals nearly the whole of the mesothorax as seen from above. The large metanotum is shaped very differently from the mesonotum, each side being concave, the anterior and posterior borders especially so. Specimens consisting of the three thoracic segments broken away from the rest of the insect and isolated on the rock are not uncommon in the limestone and can easily be recognized by the characteristic shape of the metanotum. The fore legs are decidedly short, the middle pair only slightly longer, and the hind pair much longer. The tibia of the fore leg is about 1 mm. long, while that of the middle leg is 1.2 mm. long, and that of the hind pair 2 mm. There are unquestionably five

tarsal segments in this species (as in all other members of the family Lemmatophoridae). Tillyard, who described and figured all tarsi as having only three segments, was apparently misled by the obscure condition of preservation of the fossils which he studied. Professor Dunbar and I have examined carefully the Yale specimens with particular reference to the tarsi and both of us have been unable to find any definite evidence of the number of tarsal segments in these specimens. Since several of the fossils in the Harvard collection (e. g., Nos. 3536ab and 3537) show the five tarsal segments very clearly (see figure 3, plate 2), there can be no doubt as to the number of segments. This, of course, is particularly interesting, since all known Recent Perlaria have only three segments. Tarsal claws and the empodium are well developed, as can be seen in the photograph of the tarsus of specimen No. 3536 (figure 3, plate 2).

3. Abdomen. The lateral gill-like processes on the abdominal segments can be made out in several of the Harvard specimens, although specimen No. 5147 in the Peabody Museum shows them best. These are undoubtedly vestiges of the larger and functional gills present in the nymphal stages. The cerci are long, usually much longer than the abdomen;[5] they are broad basally, but thin and delicate distally. As in Recent Perlaria the segmentation at the base is obscure, though clear beyond that point. In none of the many specimens of *typa* which I have examined are there any indications of the presence of dorsal and ventral valves, which are very obvious in Paraprisca and Lecorium.

Since the instability of the venation of *typa* has already been thoroughly discussed by Tillyard, there is no occasion for further comment on this subject, except to call attention to one variation not seen by him. That is the condition in which CuA has only two branches, CuA1 and CuA2 being united. Such a formation of the cubitus is not common in *typa* or any of the Lemmatophorinae, but is frequently found in the Parapriscinae, as I shall point out later.

Genus *Lisca* Sellards.

Lisca Sellards, 1909, Amer. Journ. Sci., (4) **26**: 163.

Fore wing: costal margin curved slightly, apex rounded; Sc close to margin for its whole length, including the base, remote from R1 and

[5] In the specimen (No. 5115) on which Tillyard based his figure of *typa* (p. 188, 1928), the cerci were broken off a considerable distance before the natural end; consequently in his drawing they are shown much shorter than in mine.

terminating beyond the base of the pterostigma; R somewhat straighter than in *typa*, there being little change in direction, if any, at the origin of Rs; Rs originating well proximad of the middle of the wing, unbranched; MA unbranched or occasionally forked; MP deeply forked, rarely three-branched or unbranched. *Hind-wing:* costal margin nearly straight, apex bluntly rounded, hind margin with a deep incision at the end of CuP; Sc nearly straight; Rs arising close to base of wing and either free from MA or coalesced with it.

Body structure: antennae long, nearly twice as long as the head and thorax combined; all segments except the first two subequal; front and middle legs short, hind legs much longer; all segments of hind tarsus short and equal in length; cerci short, only about one-half as long as the abdomen.

Genotype: *Lisca minuta* Sellards.

This genus is similar to the former in respect to the unbranched Rs and the incised hind margin of the hind wing; but it differs particularly in the proximity of Sc to the costal margin, the early origin of Rs in both wings, as well as in certain body features, such as the short cerci, long antennae, and the short and equal hind tarsal segments. The latter characteristic is unique among the known species of the family Lemmatophoridae.

Lisca minuta Sellards.

Figure 2.

Lisca minuta Sellards, 1909, Amer. Journ. Sci., (4) **26:** 163; fig. 21.
Lemmatophora minuta Tillyard, 1928, Amer. Journ. Sci., (5) **16:** 215; fig. 16–18.
Lemmatophora reducta Tillyard, 1928, *ibid.*, p. 219; fig. 19.

Fore wing: length, 4.5–7.2 mm.; width, 1.5–2.5 mm. Costal veinlets between Sc and margin weakly developed or absent altogether; pterostigmal region usually traversed by several veinlets; 5–7 weak crossveins between R and Sc; Rs arising about one-fourth the wing length from the base and free or coalesced with MA for a variable distance; MA arising proximad of the middle of the wing, usually proximad of or directly below the origin of Rs; MP usually forked almost to the middle of the wing, but occasionally three-branched or simple; CuA usually with three branches, sometimes with two or four; 1A and 2A present, both very variable in form. *Hind wing:* length, 4.5 mm.; costal veinlets apparently absent; Rs arising almost at the very base

of the wing; MA and MP unbranched; CuA forked to about half its length.

Body structure: length of body, including cerci, 6 mm.; antennae 3 mm. long, with about 28 segments;[6] cerci, 1.5 mm. long. Fore leg (preserved in specimen No. 3554), 3 mm. long; femur short and thick; first tarsal segment as long as rest of tarsus. Middle leg (preserved in specimen No. 3551), 3.5 mm. long; first and fifth tarsal segments equal, second shortest, third and fourth only a little shorter than the first. Hind leg (preserved in specimens No. 3551 and 3553),

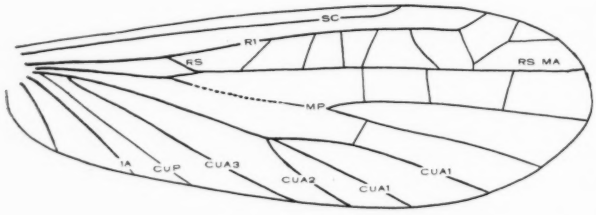

FIGURE 2. *Lisca minuta* Sellards, fore wing, showing extreme condition of coalescence of Rs and MA. Drawn from specimen No. 3568*ab*, Museum of Comparative Zoology.

4 mm. long, femur thick, tibia slender, all tarsal segments subequal in length.

The holotype of this insect was No. 916 in Dr. Sellards' collection; since that has been lost, I designate specimen No. 3551 in the Museum of Comparative Zoology, as the neotype. This was collected in the upper layer of limestone in 1934 by the writer and consists of a nearly complete insect, showing all four wings outspread, as well as most of the body, including the middle legs, one hind leg, and the cerci.

The species is not so abundant as *typa* in the limestone, but is nevertheless quite common. In the Yale collection there are 47 specimens, in the Sellards' collection 20, and in the Harvard collection 104 specimens. It is equally common in the upper and lower layers of

[6] Tillyard (1928, p. 217) states that the antennae are 3 mm. long and include about 13 segments. The fossil (No. 5210), on which he based this statement, does not appear to show the segmentation of the antennae at all satisfactorily. In two of specimens in the Museum of Comparative Zoology the antennae, also 3 mm. long, consist of 28 or 30 segments, all but the last few being very distinct.

the limestone. Of 42 specimens taken in 1932, when equal areas of the two layers were worked, 18 specimens were found in the lower layer and 24 in the upper. It is interesting to note, however, that the best complete specimens came from the upper layer. The most important of the specimens in the Museum of Comparative Zoology are as follows: No. 3551 (upper layer), consisting of the four wings, legs, cerci, and other body parts, all splendidly preserved; No. 3553ab (upper layer), wings resting back over abdomen, antennae, fore leg and hind leg preserved; No. 3554ab (upper layer), portions of wings and body; No. 3555ab (upper layer), fore and hind wings, general body structure, thorax and cerci excellent; No. 3557ab (lower layer), one very fine fore wing and portions of the thorax and abdomen; 3558ab (lower layer), fore wing and part of the body; No. 3559ab (lower layer) two fore wings, portions of the body; No. 3560ab (lower layer), general body structure, the head, antennae, hind leg and cerci excellent (wings chipped away to expose body); 3561ab (lower layer), excellent fore wing and parts of body; No. 3562ab, fore wing and part of body; No. 3563ab, two fore wings and parts of body. Nos. 3552ab (upper layer) and 3556 (lower layer) are both very fine fore wings. Of the specimens in the Sellards collection two (Nos. 263, 1015) are especially good, since they show both fore wings.

The venation of the fore wing of *minuta* is even more variable than that of *typa*, especially in the amount of fusion betwee Rs and MA, and Cu and M. In the fore wing of Sellards' original type specimen Rs and MA were coalesced for a short distance, a condition which Tillyard was unable to find duplicated in the Yale collection. He concluded, however, from the presence of a similar condition in some specimens of *typa* that this was a variable feature. That conclusion is borne out by the Harvard material, many specimens (*e. g.* Nos. 3556, 3557) of which show a variable amount of coalescence between Rs and MA. The most extreme case of this sort is in specimen No. 3568 (fig. 2), in which Rs and MA are fused for the entire length of the wing beyond their origins! Although CuA is usually free from M, it is occasionally fused with it at the base, CuA being strongly curved as it leads to the posterior margin. The shape of the fore wing is also liable to vary, some wings being much broader than the others. The coloration is another unstable feature, the wings being uniformly brown in some specimens and banded or colorless in others. Tillyard has given varietal names (such as *semitincta* and *obscurata*) to some of these individual variations, but among the fossils in the Museum of Comparative Zoology there is a complete series of intergradations

between the uniformly tinted wings and the colorless ones. He has also described another species, *reducta*, based on a fragment of a fore wing, differing from *minuta* in coloration and the structure of the cubitus, CuA being 2-branched. I do not consider this slight difference in pigmentation as specific, since it merges with other types of coloration in specimens of *minuta;* and the 2-branched condition of CuA occurs as an individual variation in every other species (*cf. typa*) of the Protoperlaria which has thus far been described.[7] I therefore consider *reducta* to be synonymous with *minuta*.

The venation of the hind wing of *minuta* is also variable, especially the amount of fusion between Rs and MA. This is clearly shown in specimen No. 3551 in the Harvard collection, which has Rs and MA coalesced in the left hind wing, but free in the right.

Generally speaking, *minuta* is smaller than *typa*, but this is not always a positive distinction. I have seen some large specimens of *minuta* with the fore wing 7.2 mm. long and some small specimens of *typa* with a fore wing only 5.5 mm. long.

Genus *Artinska* Sellards.

Artinska Sellards, 1909, Amer. Journ. Sci., (4) **26**: 163.
Artinska Tillyard, 1928, Amer. Journ. Sci., (5) **16**: 321.

Fore wing: broad, costal margin arched and apex rounded; Sc terminating well beyond the middle of the wing; R and R1 straight as far as the pterostigmal region, where there is a slight curvature; Rs arising proximad of the middle of the wing, with at least one deep fork and occasionally a small fork on one of the branches; M free from R at the base; MA usually arising slightly proximad of the origin of Rs, either free from Rs or coalesced with it, and being either simple, forked, or 3-branched; MP either simple, 2-branched, or 3-branched; CuA with the characteristic form in the family, with from 2 to 4 branches; CuR unbranched and weakly formed; 1A and 2A present, both very variable in form. *Hind wing:* costal margin arched, apex bluntly rounded, hind margin with a deep incision at the end of CuP; R1 nearly straight throughout; Rs with 2–3 branches; MA coalesced with Rs near the origin of the latter; MA and MP deeply forked; CuA well developed, either fused with M at the base or free.

Body structure: antennae (known only in *clara*) long, multi-seg-

[7] This 2-branched condition of CuA is of course brought about not by the elimination of CuA3 (= Cu1c), as indicated in Tillyard's figure, but by the coalescence of CuA1 and CuA2 (= Cu1a and Cu1b).

mented, about twice the length of the head and the thorax combined; middle legs short, the hind pair long; cerci longer than the abdomen; hind tarsus (known only in *clara*) with the first segment nearly as long as rest of tarsus.

Genotype: *Artinska clara* Sellards.

This genus, although closely allied to Lemmatophora, is easily distinguished from it by the branched Rs and the longer Sc which parallels the costal margin for most of its length. The antennae, at least in the genotype species, are much longer than those of Lemmatophora, and the prothoracic lobes apparently lack the reticulated pigmentation so obvious in *typa*. The female of both *clara* and *ovata* lacks the prominent dorsal and ventral valves present in the Aprapriscinae.

Artinska clara Sellards.

Figure 3; plate 2, fig. 5.

Artinska clara Sellards, 1909, Amer. Journ. Sci., (4) **26**: 165; fig. 25.
Artinska clara Tillyard, 1928, Amer. Journ. Sci., (5) **16**: 322; fig. 1–7 (full synonymy given here).
Estadia tripunctata Carpenter, 1926, Bull. Mus. Comp. Zool., **77**: 443.

Fore wing: length, 9.5–12.5 mm.; width, 3.5–4.5 mm.; costal margin straight for most of its length, curved only at the base and apically; apex rounded, hind margin curved distally, straight for its proximal half; Sc united with Rs at the very base, but immediately curving anteriorly towards the costal margin, which it parallels until near its termination; 12–18 veinlets between Sc and the margin; R and R1 straight, without the bend at the origin of Rs, curved only in the

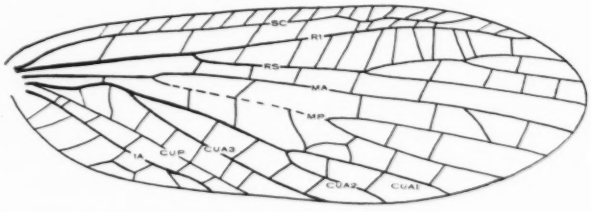

FIGURE 3. *Artinska clara* Sellards, fore wing, drawn from specimen No. 3568*ab*, Museum of Comparative Zoology.

pterostigmal region; Rs arising proximad of the middle of the wing, deeply forked and occasionally 3-branched; between Rs and R1 8–13 cross-veins; M nearly straight at the base, forking into MA and MP just proximad of the origin of Rs; MA frequently coalesced with Rs for a variable distance; CuA a very strong vein, and the numerous cross-veins between its branches are also heavy; CuP very weak, but connected with CuA and 1A by strong cross-veins.

Hind wing: length, 8.5–11.5 mm.; costal margin somewhat variable in shape, in some specimens nearly straight, in others arched; Sc close to the wing margin at the base, curving towards R and remaining closer to R than to the margin for the rest of its length; R1 very nearly straight, even in the apical region; Rs arising close to the base of the wing, coalescing for a short distance with MA and forming three terminal branches; MA forked in all specimens which I have seen; MP deeply forked to a point more proximad than the middle of the wing; CuA fused with the stem of M at the base of the wing and deeply forked to more than half its length.

Body structure: length of body, including cerci, 15 mm.; antennae 10 mm. long, about twice as long as the head and thorax combined, the first few segments short and broad, the next few about twice as long as wide, the others a little longer than broad; prothorax lobes fully as large as those of *typa*, extending even further back over the mesothorax than in that species, but completely lacking the pigmented net-work; fore legs not preserved in any specimens; middle legs short, femur 2.2 mm. long; hind leg long, femur 3 mm. long; tibia slender, 3.5–3.8 mm. long; tarsi 2.7 mm. long, the first segment nearly as long as the rest of the tarsus, the second segment equal to the combined third and fourth segments, which are equal; and the fifth equal to the second; cerci 6 mm. long, stout.

The holotype specimen of this species was No. 115 in the Sellards collection. Since that fossil has been lost, I designate as neotype specimen No. 3568ab in the Museum of Comparative Zoology; this was collected by the writer in 1932 in the lower layer of limestone and consists of a complete and splendidly preserved fore wing.

Clara is another common species in the Elmo limestone, there being 64 specimens of it in the Yale collection, 10 in the Sellards collection and 160 in the Harvard material. It is not so abundant in the upper layer of limestone as in the lower; of 64 specimens collected in 1932, when equal areas of the two layers were worked, only 21 were found in the upper layer, whereas 43 were taken in the lower. The following specimens, all from the lower layer, are the most important ones in

the Harvard collection: Nos. 3565ab, fore wing, portions of body, head, prothorax, hind and middle legs, cerci; No. 3566ab, fore wing, parts of hind wings, hind leg and cerci; No. 3567ab, two fore wings and parts of hind wing, general body structure only; 3600, both fore wings and parts of body, including head and both antennae (excellent); Nos. 3568ab, 3569ab, 3570ab, 3571ab, all fore wings, splendidly preserved.

The wing venation of this species is exceedingly variable, much more so than in *typa*. As already indicated by Tillyard, the radial sector may be either two- or three-branched; the anterior media either unbranched, two-branched or three-branched; MP either two-branched or three-branched; and CuA either two-, three-, or four-branched. In the accompanying table I have indicated the percentage of specimens in the 160 fossils in the Museum of Comparative Zoology with the various types of venation. In addition to these variations, the degree of coalescence of Rs and MA and between CuA and M is likewise unstable; in 88% of the Harvard specimens Rs and MA are free from each other, though in the remainder they are coalesced to a greater or less extent; in some they coalesce twice, the veins separating for a short space, only to join again further along. In 87% of the specimens Cu and M are free, but in the rest they are fused.

TABLE I.

DISTRIBUTION OF VENATIONAL VARIATIONS IN *A. clara*.

The figures indicate the percentage of specimens in each category.

	Rs	MA	MP	CuA
unbranched		60%		
two terminal branches	80%	26%	89%	3%
three terminal branches	20%	4%	11%	84%
four terminal branches				13%

The general habitus of this insect is similar to that of *typa*, but there are certain features of the body which are very different. The most interesting of these is in the antennae, which are perfectly preserved in one specimen (No. 3600) in the Harvard collection. They are much longer than the body and contain upwards of 110 segments, each of which bears a pair of hairs projecting anteriorly. The proximal few segments are very broad and short; the next 6 segments are about as long as broad; and the remainder are not much longer than broad. The most remarkable feature about these antennae, in addition to their large number of segments, is the presence of an enlarged

segment at regular intervals of 6 segments throughout the middle portion of the antennae. Fortunately, in the specimen mentioned both antennae are preserved and are parallel and close together, as shown in the photograph (figure 5, plate 2), so that it is possible to observe the exact correspondence of the enlarged segments in each antenna. When the fossil is examined under low power magnification, this series of enlarged segments gives the impression that in the middle portion of the antennae the segments are long and slender, since the smaller segments are not distinguishable; under high power, however, the true segmentation can be easily seen. So far as I am aware, there is nothing comparable with this condition among existing insects. It seems probable, however, that these enlarged segments were the seat of special sense organs. It is also possible that the antennae of this fossil illustrates one type of reduction in the number of segments in the insects as a whole, the joints between the small segments included in the interval between the large ones gradually disappearing.

Artinska ovata Sellards.

Figure 4.

Orta ovata Sellards, 1909, Amer. Journ. Sci., (4) **26**: 168; fig. 23.
Artinska ovata Tillyard, 1928, Amer. Journ. Sci. (5) **16**: 331; fig. 9–12.

Fore wing: length 6.5–8.5 mm.; width, 2–3 mm. Costal margin uniformly curved, apex somewhat more pointed than in *clara;* hind margin nearly straight; Sc close to R at base, straight for its entire length; 8–12 veinlets between Sc and margin; R straight at base, but curved anteriorly at the origin of Rs and usually curved posteriorly in the pterostigmal region; Rs arising proximad of the middle of the

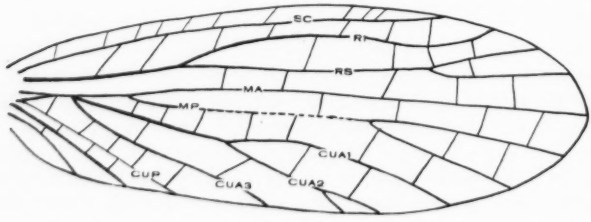

FIGURE 4. *Artinska ovata* Sellards, fore wing, drawn from specimen No. 3602*ab*, Museum of Comparative Zoology.

wing; deeply forked and occasionally 3-branched; 6–8 cross-veins between R and Rl; MA arising at about the level of the origin of Rs, not coalesced with Rs in any specimen studied thus far; MA usually simple, occasionally twigged; MP deeply forked; CuA frequently coalesced with M for a short distance. The fore wing is usually brownish in color, which is apparently due to a uniform pigmentation, although some wings are mottled with brown patches on a colorless membrane. The pattern formed in the latter case is not alike in any two specimens. *Hind wing* unknown.

Body structure: length of body, including cerci, 10 mm.; prothoracic lobes large, proportionally as large as those in *clara*. Fore legs short, 2 mm. long, the tibia 1 mm. long and the tarsus .7 mm. long (specimen No. 3575); middle legs unknown; hind legs (specimen No. 3575) long, 2 tibial spurs present, femur 1.8 mm. long, stout; tibia 2 mm. long, slender; tarsus unknown; only the 6 proximal segments of the antennae are known; these are broad, as long as wide and bear a pair of projecting spines distally, as in *clara* (specimen No. 3576).

The holotype of this species was No. 295 in the Sellards collection. Since that has been lost, I designate as the neotype specimen No. 3575ab in the Museum of Comparative Zoology; this was collected by the writer in the lower layer of limestone in 1932 and consists of a whole insect, showing especially well a fore wing, the prothoracic lobes, both front legs, and one hind leg (tarsus missing).

Ovata is similar to *clara* in most respects, but it is usually smaller, Sc of the fore wing is straight proximally (not arched as in *clara*) Rl is bent at the origin of Rs, and Rs is free from MA (in all specimens which have thus far been studied). The body structure seems to be very similar to that of *clara*, but unfortunately not much of it is known. Only a few segments of the antennae have been preserved and they are not sufficient to show whether or not the segmentation was like that in *clara*.

The species occurs commonly in the limestone, there being 30 specimens in the Yale collection and 76 in the Harvard material; it is rare, however, in the upper layer of limestone, for out of 21 specimens found in 1932, only one came from the upper layer. The following, all from the lower layer of limestone, are the most important specimens in the Harvard collection: No. 3573ab and 3601ab, complete and very well preserved fore wings; No. 3755ab, the neotype: No. 3576ab, a complete insect, showing the head, thorax, part of the antennae, and the four wings, though the venation in the hind wings is so faint that the veins cannot be followed. The latter specimen and

the neotype are the first specimens found which show any portion of the body of this species.

Although most specimens of *ovata* are much smaller than *clara*, the average length of the fore wing being around 6.5 mm., some individuals have a wing length of 8.5 mm., which is very nearly the size of small specimens of *clara*. The venation is somewhat more stable than that of other Lemmatophoridae. It is the only species of the family represented by numerous specimens in which Rs and MA are always free. In other respects, however, the venation is very variable. One specimen (No. 3602ab, lower layer) in the Museum of Comparative Zoology has a curious formation of Rl which I have not encountered in any other specimens of Protoperlaria; after the origin of Rs it arches anteriorly close to the subcosta, and then almost beneath the pterostigma, it diverges posteriorly until it almost touches Rs, finally bending anteriorly again and terminating as usual (Figure 4). Since this is the only specimen showing such a conformation, I consider it to be only an abnormal individual, rather than a representative of a new species or form.

Artinska sellardsi Tillyard.

Artinska sellardsi Tillyard, 1928, Amer. Journ. Sci. (5) **16**: 330.

Fore wing: length, 10.5–12 mm.; width, 3.6–4 mm.; costal margin curved, apex pointed; Sc united with R at the very base, straight for its entire length; R straight at the base, but bent upwards at the origin of Rs, as in *ovata;* Rs forked to about half its length; MA arising at about the level of the origin of Rs; CuA with 3 or 4 branches, either fused with M at the base or entirely free; CuP weak; anal veins unknown; cross-veins arranged as in *ovata*, though perhaps weaker.

Holotype: No. 5291a in the Yale collection, Peabody Museum, and its counterpart in the Cawthron Institute in New Zealand.

This insect differs from *ovata* only by its larger size and will perhaps turn out to be synonymous with that species. In the collection at the Museum of Comparative Zoology there is one specimen (No. 3603) which agrees in all respects with the type, except for minor individual details, such as the extra fork on R2 + 3 and CuA2. It was collected in the lower layer of the limestone in 1927 and is complete except for part of the anal area.

Subfamily PARAPRISCINAE.

Genus *Paraprisca* Handlirsch.

Prisca Sellards, 1909, Amer. Journ. Sci. (4) **26**: 167 (*nec* Prisca Fritsch, 1899).
Paraprisca Handlirsch, 1919, Denkschr. Akad.-Wiss. Wien, **96**: 45.
Paraprisca Tillyard, 1928, Amer. Journ. Sci., (5) **16**: 334.

Fore wing: narrow, costal margin curved, apex acutely rounded; Sc close to margin and parallel to it for its entire length; R straight with no curve at origin of Rs, nor at the pterostigmal region; Rs either simple or forked; MA usually unbranched, rarely forked, arising proximad of the middle of the wing; MP forked, rarely 3-branched; CuA not coalesced with M at any one point; CuP very weakly chitinized. *Hind wing:* slender; apex pointed, hind margin with a slight incision only, at the termination of CuP; Sc long, terminating near the apex; Rl straight in pterostigmal region; Rs unbranched (in all specimens studied), originating near the base of the wing; MA unbranched, MP forked; first branch of 2A deeply forked.

Body structure: antennae long, nearly twice as long as the head and thorax combined; prothoracic lobes small; all legs slender, the hind pair being exceedingly tenuate; first segments of hind tarsus as long as the others combined; cerci short. Female with dorsal and ventral valves visible externally.

The genotype of Paraprisca is *Prisca fragilis* Sellards, which until now has been the only known species of the genus. In the Harvard collection there are two specimens belonging to a second species, readily distinguished by its much larger size.

Paraprisca fragilis (Sellards).

Figure 5.

Prisca fragilis Sellards, 1909, Amer. Journ. Sci., (4) **26**: 167; fig. 22.
Paraprisca fragilis Tillyard, 1928, Amer. Journ. Sci., (5) **16**: 336; fig. 13–15.

Fore wing: length, 9–10.5 mm.; width, 2.3–3.2 mm.; Sc parallel to R for nearly its entire length, terminating near the apex; costal space with a few weak veinlets visible only in perfectly preserved specimens; R close to Sc at the base, but diverging away slightly after a short distance; Rs arising slightly proximad of the middle of the wing, either free from MA or coalesced with it; 3–5 cross-veins between Rs and MA; MA arising well proximad of the origin of Rs and unbranched

in all specimens which have been examined; 3–6 cross-veins between MA and MP; MP always deeply forked, nearly to the middle of the wing, occasionally with a short third branch; 5–8 cross-veins between MP and CuA; CuA close to M as far as the origin of CuA3, then

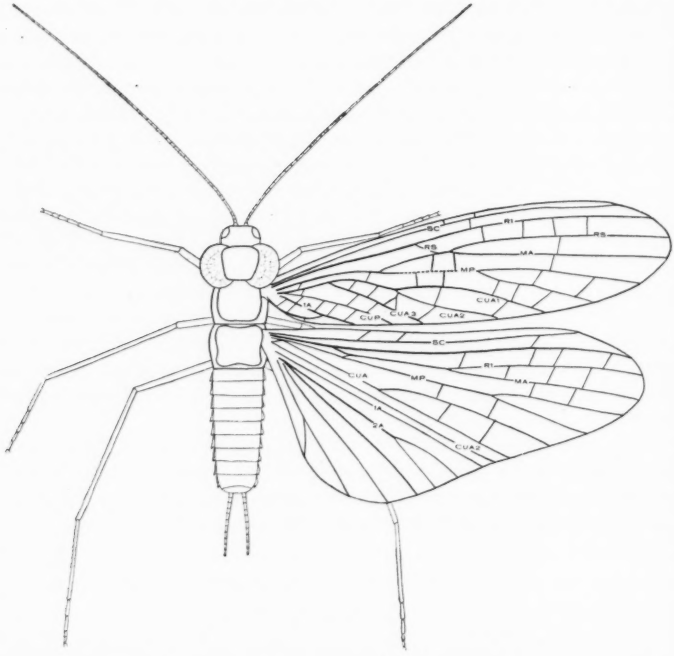

FIGURE 5. Reconstruction of *Paraprisca fragilis* (Sellards), based on specimens No. 3582*ab* and 3599*ab*, Museum of Comparative Zoology. The segments of the fore and middle tarsi are unknown; they are restored here on the basis of the segmentation in the hind tarsus (see text).

curving posteriorly; usually two cross-veins between CuA1 and CuA2, and four between CuA3 and CuA2; CuA with the three branches characteristic of the family, CuA1 terminating at about the beginning of the distal third of the wing; CuA2 terminating before the middle of

the wing; 3–4 cross-veins between CuP and 1A and 3 between 1A and 2A; 1A short variably formed; 2A very close to inner margin of wing. *Hind wing:* length 8–9 mm.; costal margin concave near mid-point; Sc is approximately mid-way between the costal margin and Rl; Rl slightly concave; Rs coalesced with MA for a short distance; CuA1 forked to mid-wing; 2A with a shallow fork.

Body structure: length of body, 5 mm. (specimen No. 3579ab); antennae 6 mm. long, the segments near the middle about three times as long as broad, those near the base of the antennae not preserved; fore leg, 3.5 mm. long, segmentation of tarsus not clear (specimen No. 3582ab); middle leg, 5 mm. long, tarsal segmentation not clear; hind leg, 6.5 mm. long, first tarsal segment very long, second and third each about one-fourth the length of the first, fourth and fifth each one-half the length of the third; cerci 1.5 mm. long.

The holotype of this species was No. 128 in the Sellards collection; since that has been lost, I designate as the neotype specimen No. 3582ab, collected by the writer in the lower layer of limestone in 1927. This specimen is nearly complete, showing the fore and hind wings out-spread, and the antennae, legs and cerci.

Fragilis is not a common species in the Elmo limestone, although there are 13 specimens in the Yale collection, 2 in the Sellards, and 36 in the Museum of Comparative Zoology. All of these fossils have been found in the lower layer of the limestone, which would indicate that the species is absent or at least very rare in the upper layer. The following are the most important specimens in the Harvard collection: No. 3582ab, the neotype, mentioned above; No. 3581ab, 3580ab, 3604ab, and 3605ab, all fine and complete fore wings; and No. 3599ab, a nearly complete insect, showing the abdominal structures especially well.

The long antennae and tenuate legs make *fragilis* the most striking of all Protoperlaria which have been found thus far. Unfortunately, the body structure is not so well known as that of Lecorium or most other members of the family Lemmatophoridae. I have attempted (figure 5) to reconstruct a figure of this insect, based upon all specimens which have been collected, in order to show the unusual habitus of the species. It has not been possible, however, for me to make out the structure of the fore and middle tarsi, or the segmentation of the antennae as a whole, since they are not preserved sufficiently well in any of the fossils; and the shape of the thoracic *nota* is likewise unknown. The other body features shown in the figure,—the long antennae, small prothoracic lobes, long legs, and the segmentation of

the hind tarsus, and short cerci,—are all definitely indicated in the fossils at hand.

The venation of the fore wing is apparently as unstable as that of other members of the family, Rs being either free or coalesced with MA, MP having either two or three branches, etc. In *fragilis*, however, as well as in *Lecorium elongatum*, the branching of Rs is subject to variation in that it may be either simple or forked.[8] CuA, although it sometimes has two as well as three branches, is apparently never coalesced with M; at least, it is not so formed in any of the 51 specimens which have been studied. Since CuA is a very strong vein, and usually well preserved, this free condition provides an easy means of recognizing the genus Paraprisca.

Paraprisca grandis, new species.

Figure 6.

Fore wing: length, 17–18 mm.; width, 4.5 mm. Sc terminating at the beginning of the pterostigma; costal space with only one or two veinlets near the middle of the wing; R nearly in contact with Sc at the base; Rs arising proximad of the middle of the wing and free from MA in the type specimens; 9–12 cross-veins between Sc and Rl; 10 between Rl and Rs; Rs forked (in types); 8 cross-veins between Rs and MA;

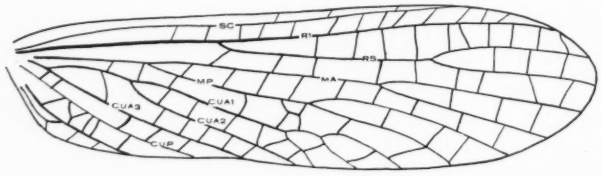

FIGURE 6. *Paraprisca grandis*, n. sp., fore wing; holotype, No. 3585*ab*, Museum of Comparative Zoology.

MA and MP diverging proximad of the origin of Rs; MA either forked or simple; MP forked to about the middle of the wing; 8 cross-veins between MA and MP and between CuA and MP; CuA1 is straight and not forked until near the wing margin; CuA1a forks a short distance beyond its origin (in the types); CuA2 very straight;

[8] This variation has much significance, since, as I shall show below, Tillyard erected the genus Sellardsia and two species upon specimens of *Lecorium elongatum* which had a forked Rs.

CuP smoothly curved; 1A very strong, nearly parallel to CuP; 2A well developed, remote from the inner margin of the wing; color of wing, uniformly light brown, due mainly to the covering of brown microtrichia.

Holotype: No. 3585ab, and paratype No. 3584ab, both collected by the writer in the lower layer of limestone in 1927, and both consisting of a complete and well preserved fore wing.

This species is close to the genotype, but can easily be distinguished by its much larger size, the fore wing being about twice as long as that of *fragilis*. It is the largest species of the order Protoperlaria which has been found. There are several venational differences between *fragilis* and *grandis*, such as the more uniform width of the wing, the shorter Sc, and the small fork on CuA1.

Genus *Lecorium* Sellards.

Lecorium Sellards, 1909, Amer. Journ. Sci., (4) **26**: 167.
Stemma Sellards, *ibid.*, p. 168.
Lecorium Tillyard, 1928, Amer. Journ. Sci., (5) **16**: 340.
Sellardsia Tillyard, 1928, *ibid.*, p. 343.

Fore wing: narrow; costal margin nearly straight, apex rounded; Sc remote from margin at base, gradually approaching it towards the middle of the wing, after which it runs parallel to the margin; R curved posteriorly slightly just before or at the origin of Rs and again in the region of the pterostigma; Rs either forked or unbranched; MA nearly always unbranched, either free from Rs or coalesced with it; MP forked, frequently 3-branched; CuA always coalesced with M, usually just before or at the separation of CuA1 and CuA2; CuA1 either simple or branched; CuP very weakly chitinized; 1A simple; cross-veins well developed, especially those in contact with CuP. *Hind wing:* slender, apex pointed; hind margin with a very slight indentation at the termination of CuP; Sc long, terminating near the apex; Rl nearly straight; Rs either unbranched or forked, originating near the base of the wing; MA unbranched, usually coalesced with Rs; MP forked; first branch of 2A deeply forked.

Body structure: antennae about as long as the head and thorax combined; prothoraici lobes larger than in Paraprisca, but not so large as in Lemmatophora; all legs stout, the hind pair long, but robust; first segment of hind tarsus as long as the others combined; cerci as long as the abdomen; female with external dorsal and ventral valves.

Genotype: *Lecorium elongatum* Sellards.

Lecorium elongatum Sellards.

Figures 7, 8, 9; plate 1, fig. 2.

Lecorium elongatum Sellards, 1909, Amer. Journ. Sci.., (4) **26:** 167; fig. 26

Stemma elegans Sellards, 1909, *ibid.*, p. 168; fig. 27.

Stemma extensa Sellards, 1909, *ibid.*, p. 168.

Lecorium elongatum Tillyard, 1928, Amer. Journ. Sci., (5) **16:** 341; fig. 16–18.

Sellardsia kansasensis Tillyard, 1928, *ibid.*, p. 349; fig. 19–20.

Sellardsia lecoriodes Tillyard, 1928, *ibid.*, p. 345; fig. 22.

Fore wing: length, 7–9 mm.; width, 2–2.7 mm.; Sc not parallel with Rl; costal space with from 5–12 well developed veinlets; R close to

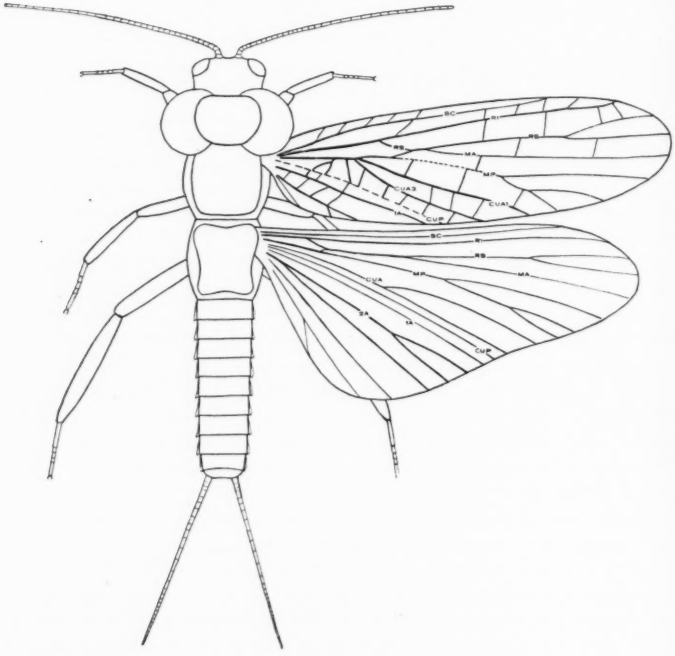

FIGURE 7. Reconstruction of *Lecorium elongatum* Sellards, based on specimens No. 3595*ab*, 3607*ab*, 3587*ab*, 3594*ab*, 3590*ab*, Museum of Comparative Zoology.

Sc at the base of the wing and also in the pterostigmal region; Rs arising proximad of the middle of the wing; 4–7 cross-veins between Rl and Sc, and 5 or more between Rs and MA; MA arising at about the same level as Rs or somewhat more distad of that point; 2–4 cross-veins between MA and MP; MP deeply forked, frequently with an extra fork on either MP1 or MP2; the amount of fusion between CuA and M is very variable, even in right and left wings of the same individual (see figure 8); 3–4 cross-veins between CuA1 and MP, and 3 between CuA1 and CuA2, and 6–8 between CuA2 and CuP; 2A is

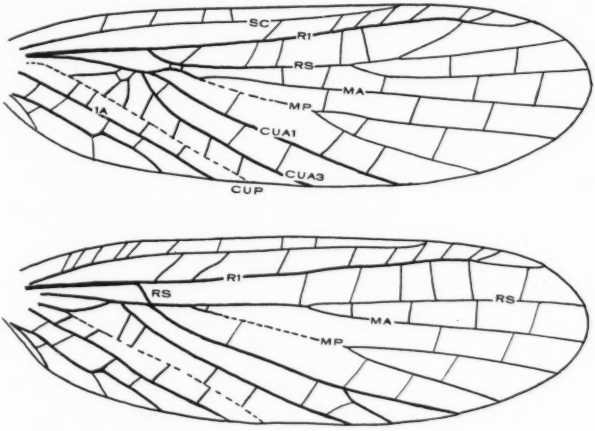

FIGURE 8. *Lecorium elongatum* Sellards; right and left fore wings of specimen No. 3587*ab*, showing differences in venation.

either simple or twigged. *Hind wing:* length, 6–8 mm.; costal margin concave over the middle part of the wing; Sc approximately mid-way between the anterior margin and Rl; Rl very slightly concave; Rs either unbranched or forked, either coalesced with MA or free from it; MP forked nearly to mid-wing; inner angle of wing bluntly rounded.

Body structure: length of body (not including antennae) 13.5 mm.; antennae 5 mm. long, the first ten segments about as broad as long, the others about twice as long as broad; length of head, 1 mm.; prothorax, 1.2 mm.; mesothorax, 1.7 mm.; metathorax, 1.8 mm.; pro-

thoracic lobes uniformly pigmented without the network found in *Lemmatophora typa;* fore legs short and stout, tibia 1 mm. long; tarsus .9 mm. long, the fifth segment the longest, the first about one-half the length of the fifth; the second, third and fourth only one-half the length of the first; middle legs twice as long as the fore, robust, femur 2 mm. long, tibia 1.8 mm. long, tarsus, 1.4 mm. long, segmentation similar to that of the fore leg; hind leg long, robust, femur 2.3 mm. long, tibia 2.7 mm. long and somewhat swollen at the middle, narrowed distally; tarsus 1.5 mm. long, the first segment a little longer than the fifth, the second, third and fourth very short. Abdomen slender, 4 mm. long; cerci 4 mm. long, very slender distally, with

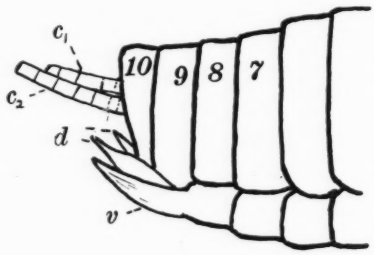

FIGURE 9. *Lecorium elongatum* Sellards; diagram of distal part of abdomen, drawn from specimen No. 3591*ab*, Museum of Comparative Zoology. c_1, left cercus; c_2, right cercus; *d*, dorsal valve; *v*, ventral valve.

about 31 segments, the first 3 being very short, the next ten much longer than broad, the remainder about as broad as long.

The holotype of this species was No. 524 in the Sellards collection; since that has been lost, I designate as the neotype specimen No. 3587ab in the Museum of Comparative Zoology; this was collected by the writer in the lower layer of the limestone in 1927 and consists of a nearly complete specimen, with the fore wings, parts of the hind wings, the antennae, thorax, abdomen, both fore legs, one middle leg, one hind leg and the cerci.

In the Yale collection there are 16 specimens of this species; in the Sellards collection 4 specimens (Nos. 441, 1272, 927, 54), all fore wings; and in the Harvard collection 46 specimens, all from the lower layer of limestone. The following are the most important of the fossils in the Harvard collection: Nos. 3597ab, 3596ab, 3598ab, 3583ab, 3592ab, 3588ab, 3606ab, all fore wings, splendidly preserved; Nos. 3595ab, a

lateral view of the whole insect, the cerci and the wings especially good; No. 3607ab, lateral view of the insect, the abdomen and cerci particularly good; 3591ab, lateral view of the complete insect, showing thorax and abdomen especially well; No. 3589ab, a dorsal view, the antennae, thoracic lobes, cerci, abdomen, fore leg and hind leg, all very well preserved; No. 3587ab, the neotype, described above; No. 3594ab, dorsal view, head, basal part of antennae and hind wing; No. 3590ab, a dorsal view of the insect, the base of the antennae, one hind leg, the cerci and the abdomen being especially good.

The wing venation of this species is more variable than that of any other Protoperlarian. The large series of well preserved specimens in the Harvard collection, added to those previously studied, has enabled us to determine more satisfactorily than before the extent of this variability. Not realizing the degree of this instability, Tillyard erected the genus Sellardsia for two new species, *kansasensis* and *lecoriodes*. He defined the genus Sellardsia simply by the statement that it differed from Lecorium only by having Rs strongly forked instead of simple. But there are several specimens in the Harvard collection possessing both of the fore wings, in one of which Rs is strongly forked but unbranched in the other (fig. 8). There can be no doubt therefore of the synonymy of Sellardsia with Lecorium. *Kansasensis*, the genotype of Sellardsia, thus becomes a very typical *elongatum*, for aside from the forked Rs it fits perfectly into even Tillyard's conception of the latter species. *S. lecoriodes* was separated from *Kansasensis* by having the apex more rounded, the origins of Rs and of the branches of CuA further apart, and 1A not quite so close to CuP; it was distinguished from *Lecorium elongatum* by having a short Rl and a more distal origin of Rs. All of these are minor venational features, which, as shown by the study of the Harvard material, differ in the right and left wings of the same specimen.

The amount of fusion between Rs and MA in the fore wing is even more variable than in Paraprisca; in some specimens the two veins are very remote from each other, whereas in others they are fused together almost to the very apex of the wing (specimen No. 3608). Specimens with these veins fused only slightly predominate, 60% of the fossils in the Harvard collection falling in this class. MA is nearly always simple, only two specimens in the Harvard collection having this vein forked. MP is two-branched in more than one-half of the specimens. The following table summarizes the data on the variation of the branching of the veins in the Harvard specimens of *elongatum:*

TABLE II.

DISTRIBUTION OF VENATIONAL VARIATIONS IN *L. elongatum*.

	Rs	MA	MP	CuA
unbranched	77%	93%	7%	
two terminal branches	18%	7%	53%	38%
three terminal branches	5%		40%	62%

The branching of CuA was in part misinterpreted by Tillyard. Observing that of the five specimens of *elongatum* in the Yale collection which possessed only a two-branched CuA, all had a three-branched MP, he concluded that the first branch of CuA (*i. e.* CuA1) had switched anteriorly and fused with MP for a very short distance, so that it now appears to be a third branch of the latter. However, in all the other common species of Lemmatophoridae (*L. typa, L. minuta, A. clara, A. ovata, P. fragilis*) a two-branched CuA and a two-branch MP sometimes occur simultaneously, a condition which in itself throws much doubt on the conclusion that MP had acquired a branch of CuA in *elongatum*. Furthermore, in the Harvard collection of the latter species, there are ten specimens which possess a two-branched CuA, and of these seven have a two-branched MP, whereas only three have a three-branched MP. If we add to this number the five fossils in the Yale collection possessing a two-branched CuA, we find that out of a total of 15 specimens possessing a two-branched CuA, 8 have a three-branched MP, and 7 have a two-branched MP. This of course is a very close approach to the equal ratio which would be expected if the loss of the branch of CuA and the addition of the third branch of MP were not correlated and their simultaneous occurrence a matter of chance.

Since no portion of the body of Lecorium has previously been known, the specimens in the collection at the Museum of Comparative Zoology have greatly advanced our knowledge of this insect and of the Protoperlaria in general. Although the wings are closer to those of Paraprisca, the body structure is much nearer to that of Lemmatophora, as indicated by the length of the antennae and cerci, as well as by the build of the leg and the tarsal structure. The formation of the prothoracic lobes is shown better in one specimen of *L. elongatum* in the Harvard collection than in any other fossil belonging to the order which has been studied. This specimen (No. 3591ab) shows the insect in a lateral view, and although the thorax is somewhat crushed, the lobes can distinctly be seen to arise from

beneath the pronotum rather than to be attached to the upper surface of the pronotum.

It was stated above that the females of Paraprisca and Lecorium possessed external dorsal and ventral valves. This assertion was based upon the interpretation of two paired processes visible in several specimens of these genera in the Museum of Comparative Zoology, and best preserved in specimen No. 3591ab (Lecorium). The chief difficulty attending the interpretation of these structures is in the determination of the sex of the insect represented. Since, however, there are no processes present in the males of the Recent Perlaria or related Orthopteroids with which we can homologize those in the fossils, I believe it most probable that the latter (at least specimen No. 3591) are females. In the photograph shown in figure 2 plate 1, I have labeled the several terminal structures on the abdomen and in figure 9 have presented a drawing of the same specimen which makes somewhat clearer than the photograph the position of attachment of these processes.[9] It will be seen that portions of both cerci are preserved in the specimen, as an examination of the obverse and reverse of the fossil immediately reveals. In the obverse (which is the half shown in the photograph) the basal and distal portions of the left cercus and a section near the middle of the right cercus are preserved. Below the cerci and apparently arising from the 9th abdominal segment are two short, paired processes, the one on the right side being partially obscured at the base by the one on the left. Further ventral are two other paired structures, the right one almost entirely hidden by the left, only the tip being visible; these appear to originate from the 8th sternum.

If we now turn to the Recent Perlaria for homologous structures, we find that, as pointed out by Walker (1919) in some species (as *Megarcys signata* Hagen) the 8th abdominal sternum is frequently bilobed posteriorly, the lobes being suggestive of vestigial ventral valves. In Pteronarcys, also, though there is no backward extension of the 8th stermum as a whole, there is a pair of slender processes near the hind margin of the segment which are considered by Walker to be true representatives of the ventral valves. It seems very probable, therefore, that the lower paired processes in the specimen of Lecorium are reduced ventral valves, not so markedly diminished in size, however, as those in Pteronarcys and other Recent Perlarians. The upper paired processes (apparently arising from the 9th sternum) are not so

[9] I am indebted to Professor G. C. Crampton for helpful suggestions concerning the interpretation of these processes.

easily explained, for in none of the existing Perlaria are there any indications of similar structures. They resemble very closely in shape the paraprocts which are well developed in many recent stone-flies (*e. g.* Pteronarcys), but in the fossil they are much too ventral to be paraprocts, unless we assume that distortion in the fossil has caused some misplacement; no such distortion, however, is suggested in the rest of the fossil. But their position is exactly that which would be held by dorsal valves, if they were present; and since the ventral valves appear to be much larger than in the existing Perlarians, it is not hard to believe that the dorsal valves were also well developed. My present interpretation of these two pairs of processes, therefore, is that the lower ones are free ventral valves, somewhat less reduced than those in Recent Perlarians; and that the upper ones are vestigial dorsal valves, which though not present in the Perlarians, are well developed in certain other groups of the Orthopteroidea, including the Protorthoptera.

The Nymphs of the Protoperlaria.

In the discussion of the ordinal characteristics of the Protoperlaria given above, it was stated that the immature stages of these insects were aquatic, and that many nymphs belonging to the order were found in the limestone with the adults. Since, however, it is not possible to correlate these nymphs specifically with the adults, I have considered it advisable to treat the nymphal forms together without attempting to place them in any of the foregoing genera.

In the collection at the Museum of Comparative Zoology there are in all 82 specimens of nymphs which belong, in my opinion, to the Protoperlaria. Of these, all but 6 inferior specimens were taken in the upper layer of the limestone, a fact which undoubtedly accounts for their apparent absence in the Yale collection, which was secured in the lower layer of the limestone.

The first question which naturally arises in connection with these immature specimens is how we are able to associate the nymphs even with the Protoperlaria, since we are obviously unable to use the rearing methods employed in dealing with the immature stages of recent insects. I believe, however, that we can cover this point definitely by the process of elimination and by a comparison of the fossil nymphs with those of the existing Perlarians.

Among the insects which occur in the Elmo limestone there are four orders which, because of their affinities with certain Recent groups, lead us to believe that they were aquatic in the nymphal

stages: the Protodonata, Odonata, Plectoptera and Protoperlaria. No nymphs of the Protodonata have ever been found in any formation, but they would certainly be at once recognized by their large size and Odonate facies. The Odonata are extremely rare in the Elmo limestone, only a half dozen insects having been found, and these are so distinctly Odonate in character that the nymphs must have been very similar to those of the Recent Odonata. The Plectoptera are common in the limestone, and because of the variety of nymphal types in the order, it is not easy to draw sharp lines between the nymphs of the Recent Plectoptera and the Perlaria, at least on such general characteristics as are preserved in the fossils. However, if we compare all available details of the fossil nymphs with those of the may-fly nymphs, it will be apparent that there are many discrepancies. The terminal abdominal appendages, for example, are characteristic nymphal cerci, short and thick, quite unlike the slender caudal filaments of the may-fly nymphs; and the broad flattened body of the fossils is very different from the slender tapering one of the may-flies. Most important of all in this connection, perhaps, is the fact that nymphs, very much like those of Recent may-flies, even in smallest details have been found in the Permian of Russia (Kargala). But when we compare the Kansan Permian nymphs with those of Recent Perlarians, we find at once such similarity that it is difficult to detect the differences which we might expect in view of the great age of the fossils. The similarities will be considered below, but it should be noted here also that the great abundance of adults of the Protoperlaria (more than 800 specimens having been collected in the limestone) is another point in favor of the conclusion that the nymphs are the immature stages of the members of that order.

In attempting to sort the eighty-two specimens of nymphs into species, we are greatly handicapped by the absence of wings, which are the principal taxonomic tool in dealing with fossil insects. Since no two specimens of the nymphs are preserved in exactly the same attitude, it is a very difficult matter to find characteristics which enable us to segregate related specimens in groups. Under such circumstances one is tempted to fall back upon size as a convenient means of correlating specimens, and although of course the size of the nymphs differs in the various instars, this procedure seems to work with some degree of satisfaction in the case of the Protoperlarian nymphs. Of the total of eighty-two nymphs, 38 are 9–10 mm. long (group A) and 41 are 4.8–5.5 mm. long (group B), only three specimens in the entire lot having an intermediate length of 7 mm. Although in all

probability some of the smaller nymphs in group B are in reality young nymphs of the species represented in group A, I believe that on the whole group B consists mainly of the nymphs of either *Lisca minuta* or *Artinska ovata,* or both; while group A consists mainly of the nymphs of either *L. typa, A. clara, P. fragilis,* or *L. elongatum,* or of all four species. In each group there are about 6 or 7 specimens which are complete and sufficiently well preserved in dorsal view to enable comparison; since I can find no structural differences between most of the well preserved fossils in their respective groups, I consider it probable that the small nymphs are chiefly one species and the large nymphs mostly one species, though it is apparently impossible to associate these with any of the species represented by the adults. I propose, therefore, to describe the best specimens in the above groups, without attempting to place them in any of the known genera.

Of the series of larger nymphs (group A) the best specimen by far is No. 3622, collected by Ruth F. Carpenter in the upper layer of limestone in 1932. This is a complete insect and is splendidly preserved. The body, which is 14 mm. long, including the cerci, is shown in dorsal aspect, but the legs, of which five are preserved, are turned in such a manner that they are seen in lateral view. This condition, which is shown in the drawing of the specimen (figure 10), gives the insect a slightly distorted appearance, but probably enables us to see more of the leg structure than would otherwise be possible. The antennae, which are 2.8 mm. long, contain 13 segments, the first being very short and broad, the next three being about as long as broad, and the rest about two and one-half to three times as long as broad. The antennae are rather broad at the base, but very slender distally. The head is rounded in front and as preserved in this fossil is two and one-half times as wide as long, although since the head is apparently bent downwards as in most adults, the true length of the head is probably much greater than it is indicated in the fossil. The eyes are well preserved in the specimen, one being distinct in the obverse and the other in the reverse; they are quite large and are situated directly above the insertion of the antennae. The thorax as a whole is long, being about two-thirds the length of the abdomen. The prothorax appears to be short and very broad, the anterior margin straight, the sides rounded, and the posterior margin slightly extended at the middle. There is no sign of the prothoracic lobes which are present in the adults of the Protoperlaria. The mesothoracic and metathoracic segments are about equal in size and similar in shape. The fore and hind wing pads are well preserved in the specimen and appear

to form a definite part of the mesonotum and metanotum, as in the case of the nymphs of most Perlaria (*e. g.*, Acroneuria). There is a

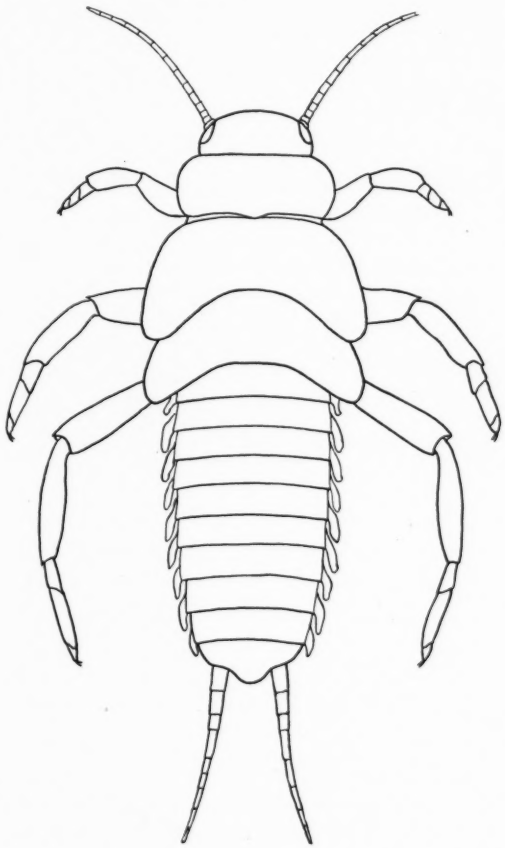

FIGURE 10. Nymph of Protoperlaria, specimen No. 3622*ab*, Museum of Comparative Zoology.

possibility, however, that the wing pads are more detached from the thorax, as in the Perlarian genera Nemoura and Leuctra, since the

basal portion of the wing pads is not very distinct in the fossil. In their general form the wing pads in the latter are shaped very much like those in Acroneuria, the apex of the wings not extending very far beyond the posterior margin of the mesothoracic and metathoracic segments. The legs, which are finely preserved in the fossil, are unusual in several respects. The fore legs are short, the middle legs somewhat longer, and the hind legs longest. Since all legs are preserved in lateral aspect, the tarsal segmentation does not stand out as clearly as in those specimens showing the legs in dorsal view, but a careful examination of them shows that there are three segments to all the tarsi. The fore leg is 2.7 mm. long, the femur and tibia each 1 mm. long, and the tarsus .7 mm.; the tarsal segments are about equal in length. The middle leg is 5 mm. long, the femur 1.5 mm., tibia 2 mm., and tarsus 1.5 mm.; the 3rd tarsal segment is the shortest, the middle one the longest. The hind leg is 6.5 mm. long, the femur 2.5 mm., tibia and tarsus each 2 mm.; the third tarsal segment is very short, the middle one very long, and the first about one-half the length of the second. Tarsal claws are present on all legs. The abdomen is 5 mm. long and 2.5 mm. wide. Ten segments are distinctly visible from above, all but the last possessing a pair of lateral gills which extend posteriorly as far as the middle of the following segment. The tenth segment is prolonged backwards to form a rounded lobe, as in most recent perlarian nymphs. The cerci are 4 mm. long, stout proximally but slender distally, and contain 8 segments. Fine hairs are present on the proximal segments of the cerci, but no hairs are visible on any other part of this nymph, even on the legs, which in most Recent Perlarians bear a series of long hairs on the tibiae and tarsi as an aid to swimming.

Specimen No. 3619ab, also found in the upper layer of limestone, is 14 mm. long including the cerci, and appears to be identical with the foregoing specimen in all respects; it shows the antennae, middle and hind legs, and cerci very well. The wing pads are especially clear, those on the right side showing definite traces of a few veins. Specimens No. 3620, 3621ab, 3623ab, 3631ab, 3632ab, 3633ab, 3634ab, 3635ab, and 3636ab, all from the upper layer, are fairly well preserved nymphs apparently identical with the two previous fossils.

The best preserved specimen of the group of small nymphs is No. 3611ab, collected by the writer in the upper layer in 1932. This is a complete specimen, 6 mm. long including cerci, showing in excellent preservation one antenna, all 6 legs, cerci, and abdominal gills. The antennae, which are 2 mm. long, contain about 18 segments, the

exact number being uncertain because a small portion of the antenna near the middle has been chipped away. As in the previous nymphs,

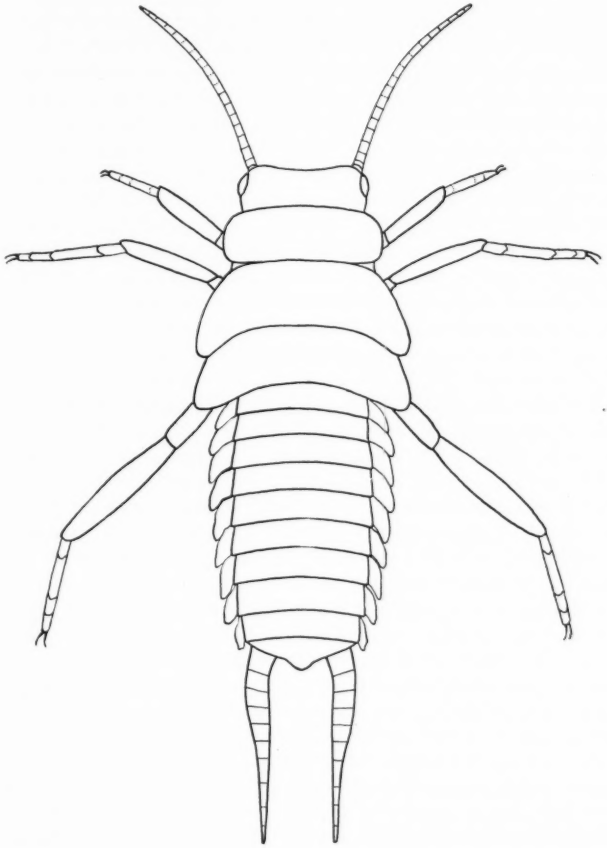

FIGURE 11. Nymph of Protoperlaria, specimen No. 3611*ab*, Museum of Comparative Zoology.

the antenna is stout at the base but slender distally. The head is apparently concave in front and as preserved is three and one-half

times as wide as long, although the true length of the head is not visible. The eyes, both of which are well preserved, are about as large as those in the previous nymphs and are similarly situated. The thorax is a little more than one-half as long as the abdomen; the prothorax short, with a slightly rounded anterior border. The wing pads are not quite as prominent as in the previous nymph, but are similar in form. The legs are fairly slender, the fore leg short and the hind leg the longest. The middle and hind tarsi are undoubtedly 4-segmented, but because of the presence of quartz crystals the segmentation of the fore tarsus cannot be determined. The fore leg is 1.3 mm. long, the tibia .8 mm. and the tarsus .5 mm. The first segment of the tarsus is the only one that can be discerned; it is a little longer than wide. The middle leg is 2.3 mm. long, the femur very short, the tibia 1 mm. long, and the tarsus 1.3 mm. long; the first tarsal segment is short, the second twice as long as the first, the third as long as the first, and the fourth about one-half as long as the third. The hind leg is 3.6 mm. long, the femur 1 mm., the tibia, 1.6 mm.. and the tarsus 1 mm.; the tarsal segmentation is similar to that of the middle leg. The tarsal claws are proportionally much larger than those of the foregoing nymphs. The abdomen is 2.5 mm. long, 1.3 mm. wide; each of the first nine segments bears a pair of lateral gills (figure 6, plate 2), proportionally much larger than those of the previous nymphs; the tenth segment is prolonged backwards to form a small lobe. The cerci are 1.8 mm. long, very slight distally but stout basally, with 10 segments, those at the base being as long as wide, the others from two to three times as long as wide.

A second well preserved specimen that appears to be identical with the above small nymph is No. 3630ab. It is 5.5 mm. long, including the cerci, and shows both antennae, one fore leg, both middle and hind legs, and cerci. The following nymphs also seem to be the same species: No. 3612ab, a complete specimen showing some of the abdominal gills very well; No. 3615ab, which has the legs and the abdomen preserved very clearly; No. 3610 and 3617ab, showing the general habitus and legs; and No. 3618ab, in which the legs are very clear. All of these were taken in the upper layer.

There is one nymph (specimen No. 3613) of about the same as the size as those in the preceding lot (6.5 mm. including cerci) which undoubtedly belongs to a very different species. Although the antennae are the same length as those of the foregoing nymphs and contain the same number of segments, the head is much larger and the cerci consist of 8 segments only, the same number as in the large

nymphs described above. The femur of the middle and hind legs is fully as long as the tibia, which is certainly not the case with the other small nymphs. The wing pads, which are very well preserved and show both hairs and veins, are much like those of specimen 3611, discussed above. The middle and hind tibiae, at least (the tarsi not being preserved), possess the series of long hairs along the posterior edge present in most Recent Perlarian nymphs; this is a characteristic which I have not seen in any of the nymphs treated in the previous pages. It seems probable, then, that there are at least three species of nymphs represented among the eighty-two specimens, but that there are only such minor differences between the species that we are unable to associate them generically or specifically with the adults.

A comparison of the structure of these nymphs with that of the adults of the Protoperlaria reveals some interesting similarities, one of which is the presence of the lateral abdominal gills on the first nine segments of the nymphs and vestigal abdominal gills on the first nine segments of the adults. As I shall point out more fully later this condition is analogous with the situation in the Recent Perlarian family Eustheniidae, the nymphs of which have functional lateral gills on the first 5 or 6 abdominal segments and the adults vestigial gills on the corresponding segments. The nymphs of some other Perlarians, also, possess indications of such gills, though they are not carried over into the adults. The cerci of the nymphs are very much like those of the adult forms, in both general structure and segmentation. The antennae are considerably shorter than in the adults and the number of segments is much smaller, as is usually the case with nymphs. The most striking difference between the nymphs and adults is the segmentation of the tarsi, there being 5 segments in the adults, but only 3 or 4 in the nymphs. In the nymphs of the Recent Perlarians there are as many tarsal segments in the nymphs as in the adults (three), but in other orders of insects (such as the Plectoptera) it is not unusual for the number of segments to be very different in the immature forms and the adults.

When we compare these Permian nymphs with those of the Recent Perlarians, we also find some interesting similarities and differences. The resemblance between the general habitus is most striking and this is likewise true of the more detailed structure of the thorax and abdomen. The antennae and cerci of the fossils, however, contain a much smaller number of segments than do those of the Recent nymphs. In the latter the antennae have from 35 segments (Chloroperla) to more than 90 (Acroneuria), and the cerci from about 15 segments

(Eustheniidae) to 50 or more (nearly all other genera). In the fossil nymphs the antennae consist of from 13 to 18 segments and the cerci from 8 to 10 segments. In this connection, however, it should be borne in mind that the adult Protoperlaria have much fewer segments in the antennae and cerci than the adult Perlaria. Aside from the difference in the number of tarsal segments, the legs of the Protoperlarian nymphs are not unlike those of the Perlaria, in which there is much diversity of structure. The lateral abdominal gills are perhaps the most interesting and important features of the fossil nymphs. As I have previously mentioned such gills are definitely absent in all Recent Perlarian nymphs, except the members of the family Eustheniidae, where they are present on the first 5 or 6 abdominal segments (Tillyard, 1921). The occurrence of these gills in the Eustheniid nymphs is an important point, since in other respects the members of this family are the most generalized of the true Perlaria. The analogy with the structure in the Protoperlarians is intensified by the fact that the adults of the Eustheniids carry over the abdominal gills in vestigial form. Although these are the only Perlarian nymphs which possess lateral abdominal gills, those of some species of Pteronarcys (e. g. *proteus*) have a pair of lateral processes on each of the first eight segments which in my opinion are modified vestigial gills. So far as I am aware no other explanation has been offered for the presence of these structures.

Relationships of the Protoperlaria.

Although in the foregoing pages I have made numerous comparisons between certain structural features of the Perlaria and the Protoperlaria, it seems advisable to summarize in conclusion the differences and similarities between these two orders, and to indicate briefly the evolution of this particular branch of Orthopteroid insects. The similarities between the two groups are so obvious as hardly to require enumeration; they are apparent in the habitus, and the general structure of the antennae, the thorax, wing venation, abdomen and cerci. Even the vestigial gills on the abdomen constitute a point of similarity, since they occur in at least one living family of the Perlaria. It is the differences in the details of the structure of the Protoperlaria and Perlaria which are more interesting and which indicate the phylogenetic relationship of the orders. The most important of these differences are as follows:

1. Tarsal segmentation. In all known Protoperlaria the tarsi are 5-segmented, whereas in all existing Perlaria they are 3-segmented.

2. Prothoracic lobes. Lateral prothoracic lobes or expansions, which are well developed in the Protoperlaria, are entirely lacking in the Perlaria, in which there is at most a broad pronotum. In this connection I again call attention to the presence of prothoracic expansions in many of the other Permian Orthopteroids.

3. Wing venation. Although the wing venation of the Protoperlaria is similar to that of the Perlaria in most respects, the presence of the posterior media (MP) in the former only is a very significant difference. It is to be noted, however, that the proximal part of MP is almost obsolete in the Protoperlaria.

4. Antennal segmentation. The antennae of the Protoperlaria with the exception of those of *Artinska clara*, contain a much smaller number of segments than in the Perlaria, usually about half the number. The condition in *A. clara*, which possesses more antennal segments than any Recent Perlarian, is also unique in having the series of enlarged segments described above.

5. Segmentation of cerci. As in the case of the antennae, the number of segments in the cerci of the Protoperlaria is less than in the Perlaria, although the difference is not so great.

6. Terminal abdominal appendages. In at least two genera of Protoperlaria the female possesses vestigial dorsal and ventral valves (if the interpretation offered above is correct), the dorsal valves being entirely absent in the Recent Perlaria and the ventral valves barely indicated in a few genera.

It is particularly significant that all of these differences, with the possible exception of the 4th, are in characteristics which are more generalized in the Protoperlaria than in the Perlaria. Aside from features which have only generic or specific rank, there are no characteristics of the Protoperlaria which appear to be more specialized than the corresponding ones in the Perlaria. I believe, therefore, that the order Protoperlaria, as defined in this paper, stands in direct evolutionary line leading to the Perlaria, although it is very unlikely that any of the genera now known were the progenitors. The fossils indicate that since the Lower Permian the evolution of this Perlarian line has resulted in the reduction of the number of tarsal segments, the elimination of the prothoracic lobes and the posterior median of the fore wing, the nearly complete loss of the vestiges of an external ovipositor and the lateral abdominal gills of the nymphs and adults. In respect to these and other features the Protoperlaria are inter-

mediate between the true Protorthoptera, for 5-segmented tarsi,[10] prothoracic expansions, an external ovipositor, and a well developed posterior media in the fore wing, were possessed by at least some of the Protorthoptera. The close relationship between the Orthoptera (*s. lat.*) and the Perlaria is now generally recognized by entomologists, and the Perlaria are frequently regarded as Orthoptera which adopted an aquatic mode of existence in the immature stages, forming a divergent branch of the Orthoptera. The Protoperlaria of the Lower Permian appear to represent the beginnings of that divergence.

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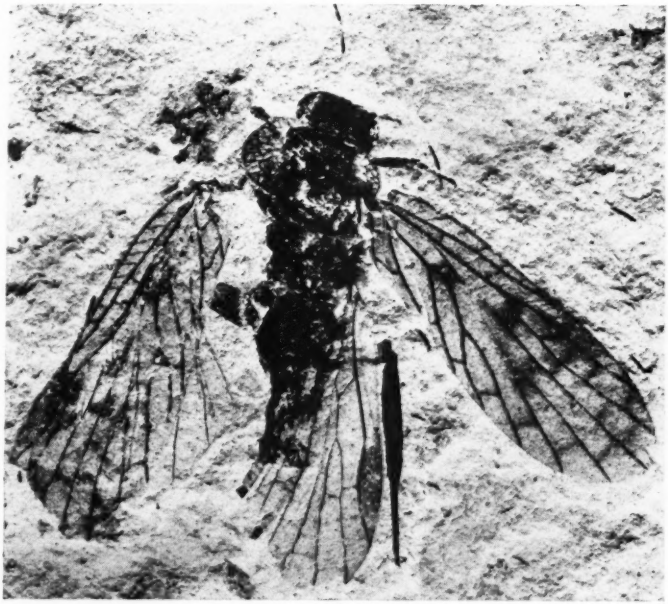
[10] In Shroeder's *Handbuch der Entomologie*, Handlirsch has given reconstructions of nine species of Protorthoptera, in seven of which he has depicted 3-segmented tarsi and in two 4-segmented tarsi. So far as I am aware, there is only one described species of Protorthoptera in which the tarsal segmentation is known,—*Protodianphipmoa* (*Cnemidolestes*) *woodwardi* Brong., from the Carboniferous of Commentry. This was described by Brongniart (Faune ent. terr. prim., 1893, p. 549; pl. 49, fig. 4) as having five tarsal segments, although in Handlirsch's reconstruction it is shown with only four segments (fig. 97).

EXPLANATION OF PLATE I.

FIGURE 1. *Lemmatophora typa* Sellards. Photograph of specimen No. 3536*a*, Museum of Comparative Zoology; length of fore wing, 6 mm.

FIGURE 2. *Lecorium elongatum* Sellards. Portion of abdomen, showing terminal appendages; length of abdomen shown (not including cerci), 2.5 mm.; *c*, cerci; *d*, dorsal valve; *v*, ventral valve.



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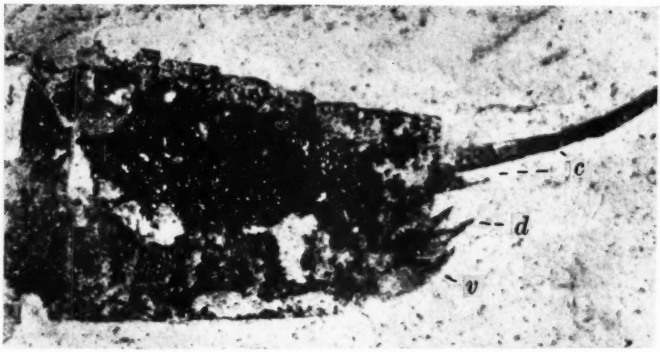

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EXPLANATION OF PLATE II.

FIGURE 3. *Lemmatophora typa* Sellards. Photograph of hind femur and tarsus, specimen No. 3536*a*. Museum of Comparative Zoology; dorsal view, showing the five tarsal segments. The short lines indicate the joints between segments. Length of tarsus, 1.5 mm.

FIGURE 4. *Lemmatophora typa* Sellards. Photograph of the femur and tarsus of specimen No. 3536, Museum of Comparative Zoology; lateral view, showing tibial spurs and the five tarsal segments. Length of tarsus, 1.5 mm.

FIGURE 5. *Artinska clara* Sellards. Photograph of antennae of specimen No. 3600, Museum of Comparative Zoology, showing the enlarged segments at regular intervals of 6 segments. The lines indicate the position of the enlarged segments; the other segments are not clearly shown in this photograph except near the end of the antennae. Length of antennae, 9 mm.

FIGURE 6. *Protoperlarian nymph*, photograph of abdomen (specimen No. 3611*a*, Museum of Comparative Zoology), showing lateral abdominal gills (*g*). The left hind wing pad is visible in the upper left corner of the photograph (*p*). Length of part of insect shown in photograph, 1.5 mm.

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